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THE INTERNAL STRUCTURE OF THE EAR  
IN SOME NOTOUNGULATES

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RESULTS OF THE FIRST MARSHALL FIELD PALEONTOLOGICAL EXPEDITION  
TO ARGENTINA AND BOLIVIA, 1922-24

The structure of the notoungulate auditory region has attracted the attention of most investigators of the order, and several accounts of the external structure have been written. The internal structure of the bulla, however, has not received the same attention. Roth (1903) published some sections, and various statements to the effect that the bulla of some forms is hollow, or probably hollow, and that the epitympanic sinus is in communication with the bulla may be found in the literature, but no general account is available. Simpson has recently published (1936) a very detailed description of the cranial structure of the Casamayor genus *Oldfieldthomasia*, which was studied by means of serial sections. Through his kindness, I was able to see a manuscript copy after work on this paper had been nearly completed. Simpson's paper covers a larger field than the present contribution, but where the two studies are on common ground our interpretations are in close agreement.

I was attracted to this subject by the accidental breakage of a *Hegetotherium* skull which revealed the presence of a septum in the bulla. From this beginning a study was made of representative genera from such families as were available in the Field Museum collections, in an endeavor to determine whether the middle ear structure threw any light on problems of taxonomy and phylogeny. The following contribution is by no means complete, since several families are not represented, but it is hoped that it may serve as a working basis. The majority of the specimens sectioned are from the Santa Cruz beds. Material from this horizon is particularly suitable for detailed investigations, due to the excellent preservation of the bone and the softness of the matrix.

I wish to express my sincere thanks to Mr. Elmer S. Riggs for permission to section the specimens in the Field Museum collections, and to Dr. Walter Granger for similar permission in regard to the American Museum specimen of *Pseudotypotherium*. The drawings are the work of Mr. Carl F. Gronemann, Staff Illustrator, Field Museum. I am indebted to Mr. James H. Quinn for his skillful preparation of the *Homalodotherium* specimen.

### Suborder Typotheria Zittel

### Hegetotheriidae Ameghino

#### Hegetotherium Ameghino (fig. 44).

The description is based mainly on F.M. No. P13194, referred to *H. mirabile* Ameghino. The specimen was collected by Mr. Riggs in the Santa Cruz beds on the Atlantic coast some twenty miles south of the Río Coyle inlet, Santa Cruz, Argentina.

The bulla is partially divided into two cavities by a vertical antero-posteriorly aligned septum. This septum is low and attached anteriorly, ventrally, and posteriorly to the walls of the bulla. Beneath the promontorium it is free, leaving a rather large opening between the two chambers. From its relations, this septum could well be regarded as a true septum bullae formed by union of ecto- and entotympanics (see p. 222 for a discussion of this question). The medial chamber of the bulla—the hypotympanic sinus—is smaller and much shallower dorso-ventrally than the lateral—the tympanic cavity. It is hollow, oval in horizontal section, and somewhat deeper than wide. The anterior extremity of its wall is thickened. The tympanic cavity is much deeper than wide, rounded laterally, and tapering anteriorly. The anterior half of the cavity, at least as far back as the tympanic aperture of the facial canal, is roofed by the tympanic. The Eustachian tube is therefore entirely surrounded by this element, except possibly at its extreme outer margin where it seems to open between tympanic and alisphenoid. The tube runs antero-internally and is situated lateral to the anterior part of the septum; it opens externally a little below and behind the foramen ovale. The wall of the bulla is closed below the tube, and there is no indication of a styloform process. The recessus epitympanicus is of medium size, and the pneumatic foramen is relatively much larger than that of *Nesodon*. There is a small recess anterior to this foramen. The sulcus tympanicus is large and well defined, and the crista tympanica prominent. The recessus meatus is shallow.



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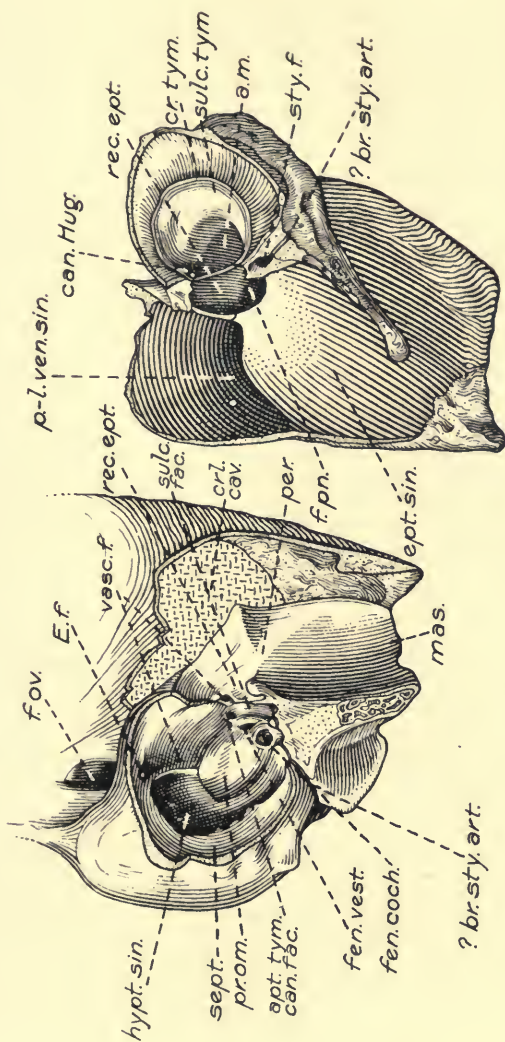


FIG. 44. *Hegelertherium mirabile* Ameghino. F.M. No. P13194. Auditory region of left side longitudinally sectioned and the two halves reflected. Dotted areas represent sectioned bone; the cranial cavity is filled with matrix. For abbreviations see page 227.  $\times 2/1$ .

The promontorium in this and the other typotheres studied is large. It forms a large part of the medial wall of the tympanic cavity and a small part of the roof of the hypotympanic sinus. The fenestra cochlearis is round and faces posteriorly; the fenestra vestibuli is oval with the long axis aligned antero-posteriorly, and faces laterally.

The details of the carotid circulation are somewhat uncertain in the forms described here. In *Hegetotherium*, Sinclair (1909, p. 74) identified as the aperture of the carotid canal a foramen which notches the basioccipital near the mid-line of the bulla. In the specimen under consideration, this foramen leads anteriorly into a canal which runs between the medial wall of the bulla, the ventro-medial margin of the periotic, and the basioccipital. This canal opens into the cranial cavity at the anterior extremity of the periotic. This internal orifice occupies approximately the same position on the inside of the skull as the sectioned canal identified as the carotid by Simpson (1933, fig. 1) occupies on the brain cast. The evidence in favor of regarding this foramen and canal as being for the internal carotid seems to be sound. In P13194 I have detected a small groove in the posterior external wall of the bulla between the tympanic and periotic. This apparently continues medially beyond the foramen lacerum posterius (broken away in the specimen) into a minute foramen in the periotic situated just above the groove for the basioccipital between the periotic and the medial wall of the bulla. Laterally this groove continues into the tympanic cavity between the squamosal and tympanic, ending at the internal orifice of the stylomastoid foramen. At first I thought that this groove might have lodged a minute stapedial artery (pterygopalatine portion of the internal carotid) which would therefore have branched off from the internal carotid outside the bulla. However, after finding the apparent medial extension of this groove to the periotic and noting its lateral connection with the stylomastoid foramen, I am inclined to believe that it more probably lodged some branch of the stylomastoid artery (in man a branch of the posterior auricular). Two small unidentified foramina, probably vascular, that leave the tympanic cavity, have been noted. One of these pierces the tympanic in front of the promontorium and the other leaves the cavity opposite the apertura tympanici canalis facialis.

The venous sinus in the squamosal is well shown on the figured specimen anterior to the epitympanic sinus. It is partially enclosed medially by the lateral face of the periotic. Essentially the same foramina open into it as in *Adinotherium* (p. 214).

The course of the facial nerve (VII) is very clear in this specimen and appears to be similar to that described by Simpson in *Oldfieldthomasia*. The canalis facialis opens internally into the dorsal portion of the internal auditory meatus directly above the orifice for the auditory nerve (VIII), from which it is separated by a low horizontal septum. Within the periotic, the canal is joined by the hiatus facialis for the great superficial petrosal nerve, which enters the bone on its anterior face near the junction with the tympanic. The facial canal opens into the tympanic cavity a little above and anterior to the fenestra vestibuli. The orifice is bounded dorsally by the tympanic and ventrally by the periotic. From the aperture a sulcus facialis runs backward and slightly outward to the internal orifice of the stylomastoid foramen. The latter is situated between the tympanic and squamosal above the posterior "leg" of the sulcus tympanicus. The external opening of this foramen is the same as in other notoungulates previously described (Patterson, 1932). The canal of Huguier for the chorda tympani begins internally between the tympanic and squamosal above the anterior "leg" of the sulcus tympanicus. It opens externally at the posterior extremity of the fissura Glaseri. The position of the external orifice is constant in all notoungulates that I have examined.

**Pachyrukhos** Ameghino (fig. 45).

The following account is based on F.M. No. P12994 collected by Mr. J. B. Abbott in the Santa Cruz beds at Killik Aike Norte, Río Gallegos, Santa Cruz. It is referred to *P. moyani* Ameghino.

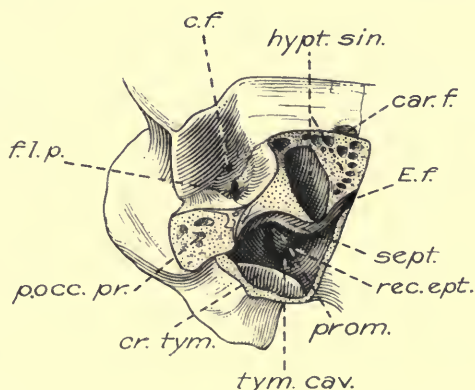


FIG. 45. *Pachyrukhos moyani* Ameghino. F.M. No. P12994. Antero-ventro-lateral view of auditory region of left side. Dotted areas represent sectioned bone. For abbreviations see page 227.  $\times 2/1$ .

The bulla differs in shape and proportions from that of *Hegetotherium*, being much deeper dorso-ventrally and having a somewhat greater transverse, than antero-posterior, diameter. The auditory meatus is longer and inclined more dorsally. These departures from the more generalized type exemplified by *Hegetotherium* are, of course, accompanied by changes in internal proportions. The hypotympanic sinus is smaller than the tympanic cavity and is more antero-internal in position, the septum is aligned antero-externally postero-internally, and the tympanic cavity is much deeper and more dorsal in position than the hypotympanic sinus. Posteriorly, it extends back above the paroccipital process.

Apart from proportions, however, the middle ear structure of the two genera is essentially similar. The carotid circulation appears to be the same in each; both have a prominent crista tympanica, and a rather low vertical septum. Neither has a styliform process. The most noticeable distinction in *Pachyrhinos* is the secondarily thickened, cellular anterior and medial walls of the hypotympanic sinus. In this character the genus parallels *Protypotherium* and the typhotherids, but the cellulae are more circular and have much thicker walls.

#### Interatheriidae Ameghino

##### *Interatherium* Ameghino (fig. 46).

F.M. No. P13057, referred to *I. robustum* (Ameghino) and collected by Mr. G. F. Sternberg in the Santa Cruz beds at Killik Aike Norte, Río Gallegos, Santa Cruz, clearly reveals most of the middle ear structure.

The bulla is approximately quadrangular in horizontal section. The hypotympanic sinus is hollow and considerably smaller than the tympanic cavity. A remarkable feature, in comparison with the hegetotherids, is the lack of a septum partially separating the two chambers. However, small vertical ridges which may be vestiges of this structure are present medial to the Eustachian tube and the posterior carotid foramen. These ridges occupy the same positions as the anterior and posterior extremities of the septa of *Hegetotherium* and *Pachyrhinos*. This might indicate that the septum had been present in the early members of the family but became reduced in the course of later evolution.

The tympanic cavity is broader and much deeper than the hypotympanic sinus; it is roughly rectangular with the greatest diameter in the antero-posterior direction. The Eustachian tube extends



antero-internally and is entirely surrounded by the tympanic. It opens externally below a shelf, formed by the tympanic, which projects above it for a short distance. The anterior wall of the hypotympanic sinus is vertical and meets this shelf at a right angle, an arrangement peculiar to this genus. There is no styloform process but, to judge from *Protypotherium*, I am inclined to regard the lack of it as secondary. Above and on the medial side of the

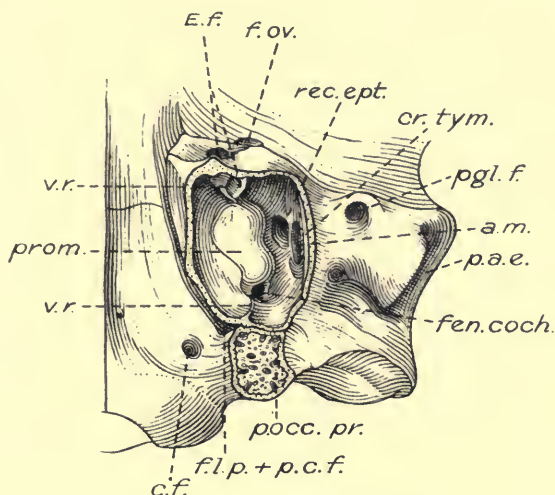


FIG. 46. *Interatherium robustum* (Ameghino). F.M. No. P13057. Ventral view of auditory region of left side. Dotted areas represent sectioned bone. For abbreviations see page 227.  $\times 2/1$ .

internal opening of the Eustachian tube there is a recess leading antero-internally. In *Protypotherium* two foramina lead from this recess; it is probable therefore that the same condition prevails in this genus. The recessus epitympanicus is similar to that of *Hegetotherium*, and the pneumatic foramen, as in that genus, is approximately half as large as the internal opening of the external auditory meatus. The sulcus tympanicus is larger and deeper than in the hegetotheriids, but the crista tympanica on the other hand is much less prominent. The recessus meatus, as in all the forms herein described, is very shallow.

The carotid circulation in this, and in the remaining forms described, differs decidedly from the arrangement seen in the Hegetotheriidae in that the internal carotid traversed the bulla instead of passing forward medial to and outside it. In *Interatherium* the

posterior carotid foramen is small and situated on the lateral side of the foramen lacerum posterius.<sup>1</sup> It opens into the tympanic cavity lateral to and above the posterior vertical ridge (remnant of the septum?). I have not detected any arterial foramen leaving the cavity but it is very probable that the recess above the Eustachian tube ends in a foramen or foramina (see below under *Protypotherium*).

The venous foramina and sinus, and the courses of the facial nerve and chorda tympani offer no peculiarities.

**Protypotherium** Ameghino (fig. 47).

The figured specimen, F.M. No. P13002, was collected by Mr. Sternberg in the Santa Cruz beds at Killik Aike Norte, Río Gallegos, Santa Cruz. It is referred to *P. australe* Ameghino.

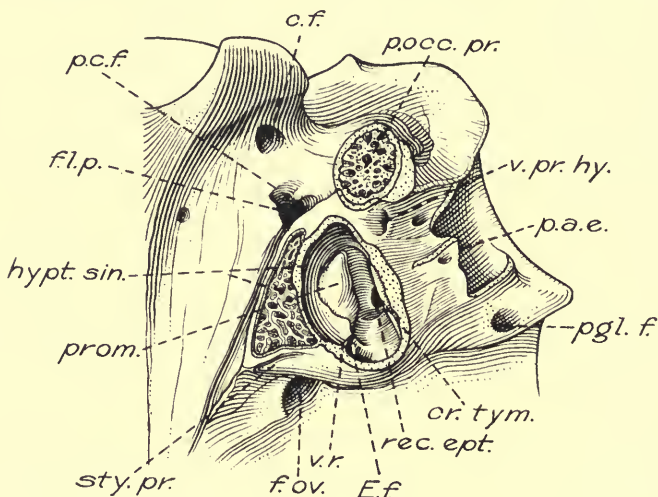


FIG. 47. *Protypotherium australe* Ameghino. F.M. No. P13002. Ventral view of auditory region of left side. Three elements may be seen participating in the base of the paroccipital process, the exoccipital forming the major part, the tympanic anteriorly, and the posterior adventitious bone laterally. Dotted areas represent sectioned bone. For abbreviations see page 227.  $\times 2/1$ .

This genus agrees with *Interatherium* in nearly all points of structure. The following distinctions have been noted: The posterior vertical ridge is lacking. The external opening of the Eustachian tube is not widely open below, nor is it provided with a shelf-like roof above. The reason for this is that the anterior wall of the tympanic

<sup>1</sup>In an earlier description of the interatherid *Plagiathrus* (= *Argyrohyrax*) I incorrectly figured the posterior carotid foramen as being internal to the foramen lacerum posterius (1932, fig. 5a).

cavity sends a styliform extension medially, and a little anteriorly and ventrally to underlie the anterior extremity of the hypotympanic sinus. It is demarcated from the ventral wall of the sinus by a groove. The sinus continues beyond it in an antero-internal direction. Morphologically, this extension seems to be a styliform process, but it is very different from the freely projecting processes characteristic of the Toxodonta and *Homalodotherium*. The medial wall of the hypotympanic sinus is cancellous and secondarily expanded in *P. australe*. It extends very nearly to the lateral extremity of the sinus. The cancelli are very fine and differ considerably from the thicker and more regular filling of the expanded medial wall in *Pachyrhinos*.<sup>1</sup> The cancellous portion is shallow dorso-ventrally.

The posterior carotid foramen is in the same position as in *Interatherium*. At the anterior end of a small recess above and medial to the Eustachian tube, homologous with the larger recess in *Interatherium*, are the tympanic apertures of two small foramina. The medial foramen of this pair is situated at the anterior end of the promontorium between the periotic and tympanic, and leads antero-internally to the cranial cavity. Its cranial orifice is situated above and behind the foramen ovale and is bounded medially by the periotic, laterally by the tympanic and alisphenoid. I regard this as the anterior carotid foramen. The smaller lateral foramen tunnels the tympanic in an anterior direction, emerging externally above the orifice of the Eustachian tube and below the foramen ovale. This foramen is almost certainly vascular and possibly may have transmitted the stapedia artery. An equally possible alternative, however, is that the arteria promontorii was suppressed, the medial (anterior carotid) foramen transmitting the stapedia artery and the lateral its ramus inferior. The position and courses of these foramina differ somewhat from the foramen regarded as anterior carotid in *Oldfieldthomasia* by Simpson (1936, pp. 16-17). Complete uniformity can hardly be expected, however, among all forms in which the carotid traversed the bulla. The vagina processus hyoidei terminates in a minute foramen, probably vascular, which pierces the tympanic in an antero-dorsal direction. I have not been able to trace it completely.

<sup>1</sup>This character is not common to all species, however. In a skull referred to *P. attenuatum* Ameghino, F.M. No. P13050, the medial wall of the sinus is neither expanded nor cancellous, and the medial portion of the sinus is deeper than in P13002.

## Typotheriidae Lydekker

*Pseudotypotherium* Ameghino (fig. 48).

The description is taken from A.M. No. 14509 from the Monte Hermoso beds at Monte Hermoso, Buenos Aires. The specimen is identified as *P. pseudopachygnathum* (Ameghino).

In the external characters of the auditory region the typotherids bear some resemblance to the earlier toxodontids. The two families have in common the high porus acusticus externus, the prominent crista meati with its descending spine, and the lip from the crista which forms the ventral border of the porus. The tympanic cavity

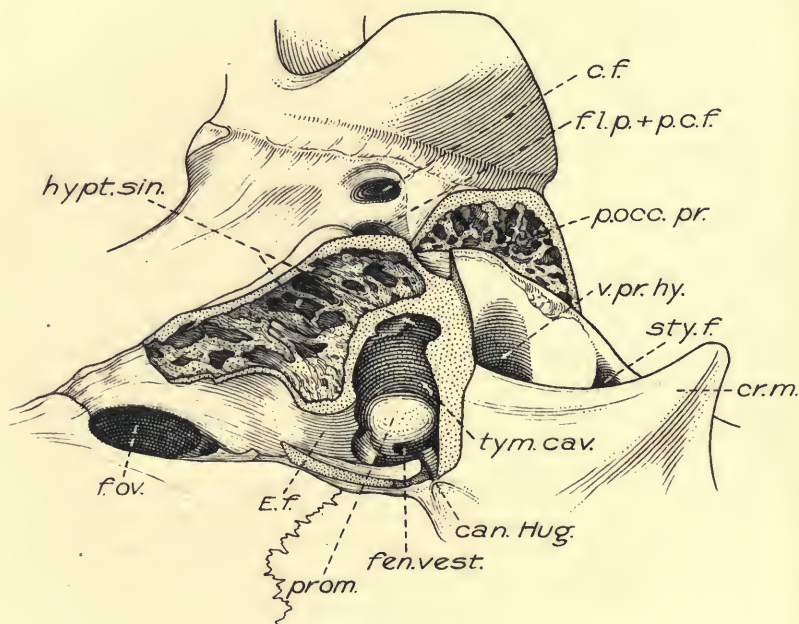


FIG. 48. *Pseudotypotherium pseudopachygnathum* (Ameghino). A.M. No. 14509. Ventro-lateral view of auditory region of right side (crista meati restored from left side). For abbreviations see page 227.  $\times 3/2$ .

is situated relatively high on the side of the cranium, the greater part of it dorsal to the hypotympanic sinus, and the Eustachian tube is deep dorso-ventrally in each. These purely convergent resemblances, possibly conditioned in part by the high porus acusticus externus in each family, end here, however. Structurally, the typotherid middle ear is a derivative of the interatherid type, such



as that seen in *Protypotherium australe*, a fact of considerable taxonomic and phylogenetic interest (see p. 224).

The hypotympanic sinus is ventral in position, its lateral portion being below part of the tympanic cavity. It is rather shallow dorso-ventrally at its medial extremity. The medial wall seems to have expanded laterally, as in *Protypotherium australe*, until it has filled a major part of the cavity. The filling is cancellous, the cancelli resembling those of *P. australe* and not those of *Pachyrhinos*.<sup>1</sup> The ventral wall of the sinus forms the ventral wall of the bulla.

The tympanic cavity is similar in shape to those of the interatherids. As in *Protypotherium*, only the anterior vertical ridge (remnant of the septum?)—the part forming the medial wall of the Eustachian opening—remains. The tube (not detected when the external structure was described) is entirely surrounded by the tympanic, as in the forms previously described; its external orifice is very deep dorso-ventrally. A styliiform process similar to, but larger, deeper and less distinctly differentiated than that of *Protypotherium*, is present. The recessus epitympanicus and the pneumatic foramen are relatively smaller than in the interatherids. *Pseudotypotherium* differs from *Interatherium* and *Protypotherium* in having a shallower sulcus tympanicus, but agrees with them in having a weak crista tympanica.

The position of the posterior carotid foramen in the posterior wall of the bulla has already been described and figured (Patterson, 1934a). Neither the anterior carotid foramen nor the tympanic aperture of the facial canal can be seen, probably as a result of slight distortion. The openings of the various venous foramina have been described previously. Their arrangement is similar in all essentials to the pattern characteristic of the order. The canal of Huguier for the chorda tympani and the internal orifice of the stylomastoid foramen are visible and in their usual positions.

### Suborder Toxodonta Owen

#### Toxodontidae Gervais

*Nesodon* Owen (fig. 49).

The following account is chiefly based on F.M. No. P13105, a young individual referred to *N. imbricatus* Owen. The specimen

<sup>1</sup> In a previous paper on the external characters of this specimen (1934a, p. 84) I stated that the hypotympanic sinus was cancellous. The section shows that this is not strictly correct since only the expanded medial wall shows this condition.

was collected by Mr. Abbott in the Santa Cruz beds on the Atlantic coast twenty miles south of Río Coyle, Santa Cruz.

Scott (1912, p. 137) has given a good account of the external appearance of the bulla in young and adult specimens.<sup>1</sup> In young individuals it is bladder shaped, and the long axis is directed antero-posteriorly; in adults it has a mammillate shape, and the long axis is dorso-ventral. These changes in external appearance are accompanied by internal changes, as will appear below in the description of an adult specimen of the closely related *Adinotherium*. In both young and old individuals the antero-internal corner of the bulla extends forward in a flat triangular plate which overlies part of the alisphenoid, and there is a conspicuous styliform process extending antero-internally from the lateral wall.

The bulla as a whole has a dorso-ventro-internal alignment; the hypotympanic sinus being ventral and somewhat medial and anterior to the tympanic cavity. The hypotympanic sinus is hollow and egg-shaped with the narrow end pointing forward. The plate overlying part of the alisphenoid, which was mentioned above, is formed by an extension of its anterior wall. The walls of the sinus form the greater part of the exposed portion of the bulla. The sinus is partially separated from the tympanic cavity by an inconspicuous septum. This structure is much smaller than the corresponding one in the hegetotherids, being little more than a ridge. It is situated ventral to the sulcus tympanicus and is thus almost horizontal—a further difference from the hegetotherid septum.

The tympanic cavity is approximately equal in volume to the hypotympanic sinus, but is much more irregular in shape. A recess extends medially above the posterior extremity of the sinus behind the opening into this cavity. A second, much smaller recess extends anteriorly on the inner side of the medial wall of the Eustachian tube. The anterior carotid foramen opens into this cavity, as in the interatherids. The Eustachian tube is large, situated at the anterior extremity of the tympanic cavity, and opens externally below the posterior portion of the very large foramen ovale. It is surrounded by the tympanic. The lateral wall of the tympanic cavity is very thick and dense, and projects freely in an antero-internal direction as the laterally compressed styliform process—a great contrast to the decidedly sessile process of the interatherids and typotherids.

<sup>1</sup>It should be noted that Scott identified the bony plate which separates the postglenoid and post-tympanic processes of the squamosal, and unites with the lateral wall of the bulla, as a part of the mastoid process. Actually this plate is the crista meati of the tympanic.

Below the Eustachian tube the styliform process and the lateral wall of the hypotympanic sinus do not fuse. The recessus epitympanicus is fairly deep, and the foramen pneumaticum is small in comparison with the size of the hypotympanic sinus. The sulcus tympanicus is poorly defined and very shallow; it is inclined ventro-

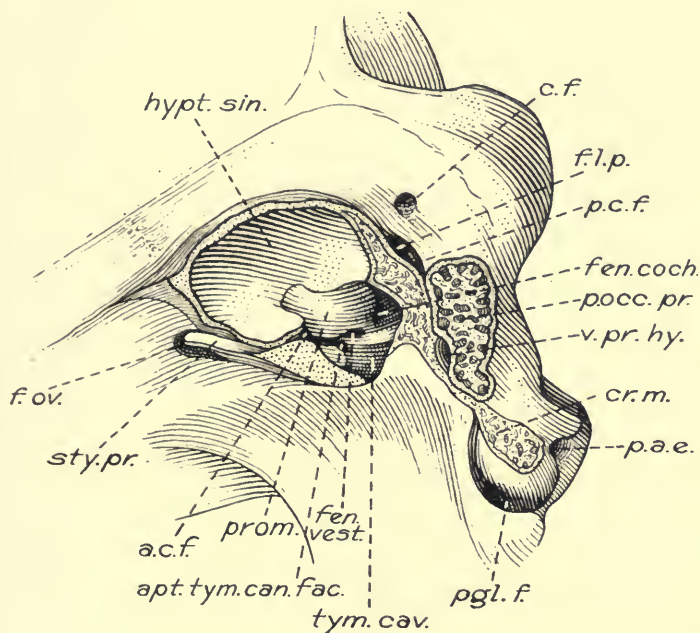


FIG. 49. *Nesodon imbricatus* Owen (juv.). F.M. No. P13105. Ventro-lateral view of auditory region of right side. Dotted areas represent sectioned bone. For abbreviations see page 227.  $\times 1/1$ .

internally and situated directly above the septum. A faint ridge is the only vestige of the crista tympanica. The recessus meatus is shallow. The promontorium is large, and the fenestra vestibuli and fenestra cochlearis are similar to those of the forms previously described.

The posterior carotid foramen is quite large and is situated in the posterior wall of the bulla lateral to the foramen lacerum posterius. As in all forms described here, hegetotherids excepted, both foramina share a large common external orifice. The posterior carotid entered the bulla lateral to the recess above the posterior extremity of the hypotympanic sinus, its orifice being separated from the recess by a vertical ridge of bone. No sulcus caroticus can



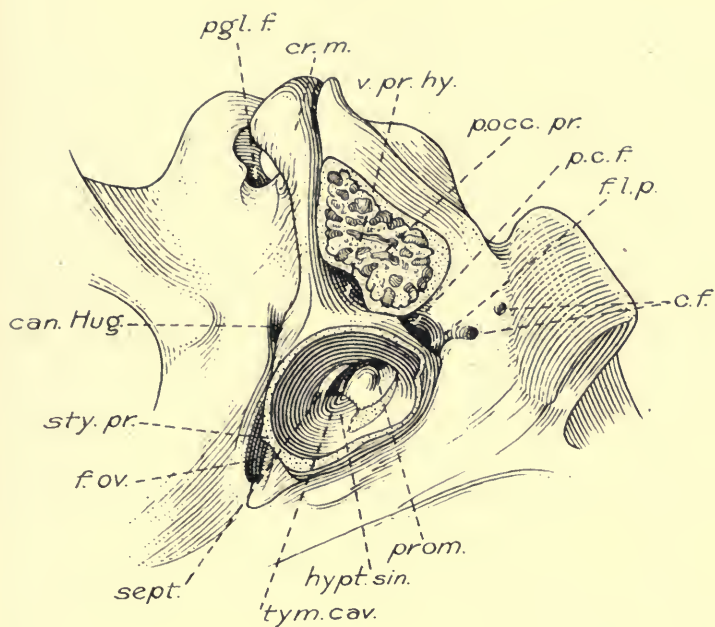
be detected. At the anterior extremity of the promontorium, and medial and slightly posterior to the internal orifice of the Eustachian tube, is a rather large foramen, deep dorso-ventrally, which leads antero-internally to the cranial cavity to open there into a recess near the exit of nerve V<sup>3</sup>. I regard this as the anterior carotid foramen. At its tympanic orifice it is bounded medially by the periotic and laterally by the tympanic (and possibly by the alisphenoid also, although this point can not be determined certainly from the specimen). This foramen is undoubtedly homologous with the one similarly situated in *Protypotherium*. I have not seen any foramen corresponding to the "lateral" foramen of *Protypotherium* described above. There might, however, be such a structure within a small recess above and behind the Eustachian tube.

The apertura tympanici canalis facialis opens at the posterior extremity of the small recess just mentioned. As in *Hegetotherium*, it is slightly dorsal and anterior to the fenestra vestibuli and is bounded above by the tympanic, below by the periotic. A sulcus facialis was present but the posterior part is not preserved in the specimen. The internal orifices of the stylo mastoid foramen and the canal of Huguier appear to be in the same positions as in *Hegetotherium*.

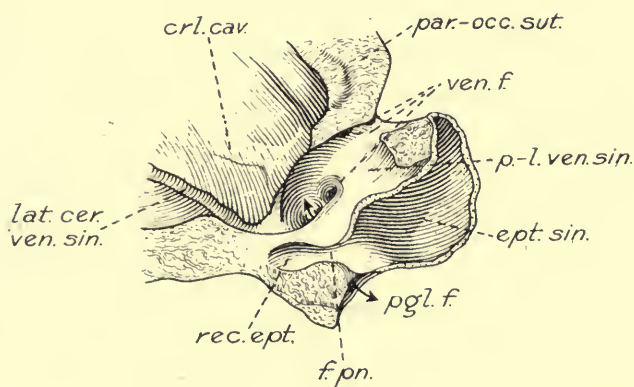
#### *Adinotherium* Ameghino (fig. 50).

The description is taken from F.M. No. P13110, a young adult referred to *A. ovinum* (Owen) and collected by Mr. Abbott in the Santa Cruz beds on the banks of the Río Coyle inlet, Santa Cruz.

As stated above, there are some interesting differences in proportion from the young *Nesodon*. The hypotympanic sinus is oval in shape with its long axis in the dorso-ventral direction, thus conforming to the external shape of the bulla. In correlation with the increase in depth of the hypotympanic sinus in the adult, its wall forms a greater part of the lateral wall of the bulla than it does in young specimens. The tympanic cavity appears to be relatively smaller in comparison with the size of the hypotympanic sinus than in the young *Nesodon*, and is even more dorsal in position. In adult toxodontids, therefore, there are three chambers one above the other participating in the auditory structure—the hypotympanic sinus, the tympanic cavity, and the epitympanic sinus. With regard to the function of the sinuses I can do no more than follow the suggestion of Gregory (1920, p. 164) that the hypotympanic sinus probably functioned as an organ of resonance. Structurally, the bulla of the adult *Adinotherium* differs so little from that of the young



a



b

FIG. 50. *Adinothierium ovinum* (Owen). Dotted areas represent sectioned bone. For abbreviations see page 227.  $\times 1/1$ . a, F.M. No. P13110. Ventral view of auditory region of left side. b, F.M. No. P13107. Ventro-medial view of section showing sinuses.

*Nesodon* that description is unnecessary. The styloform process is generally more reduced in *Adinotherium*.

A very young specimen of the same species, F.M. No. P13107, collected by Mr. Abbott five miles south of Coy Inlet shows some interesting details. The bulla, periotic, basioccipital, occiput, and part of the squamosal are missing. The resulting section shows perfectly the large hollow epitympanic sinus and the relatively small foramen pneumaticum connecting it with the recessus epitympanicus. Also, antero-medial to the epitympanic sinus appears the large venous sinus into which open the various vascular foramina bordering the squamoso-parietal suture, the postglenoid foramen, the mastoid foramen, and the large cerebral venous sinuses, to be described in another paper of this series, one of which is particularly well shown on this specimen. The epitympanic sinus is surrounded by this venous system but is not perforated by any member of it. Simpson has described similar conditions in *Oldfieldthomasia* (1936, pp. 27, 28).

### Notohippidae Ameghino

#### Rhynchippus Ameghino.

Three specimens belonging to this genus are available, F.M. Nos. P13410 and P13420 referred to *R. equinus* Ameghino, and A. M. No. 29555 referred to *R. pumilus* Ameghino, but no one of them is in a condition to permit detailed study. The first two were collected by Mr. Abbott, the third by the first Scarritt Expedition; all are from the Deseado beds at Cabeza Blanca, Chubut, Argentina.

The major structural features appear to be essentially similar to those of *Nesodon* and *Adinotherium*. There is a large hollow hypotympanic sinus which is ventral in position, and a smaller, more dorsal tympanic cavity. The hypotympanic sinus conforms to the external shape of the bulla and is approximately equal in length and depth. The anterior extremity of the wall is thickened. The internal faces of the walls are smooth in *R. equinus*, but in *R. pumilus* they bear a number of thin bony ridges. The posterior carotid foramen opens into the posterior wall of the bulla. No further details of the carotid circulation can be detected in the specimens available. In a previous description of the external structure of the auditory region of *R. equinus*, F.M. No. P13410 (Patterson, 1932, p. 13, fig. 3a), an opening was shown between the bulla and basioccipital a little anterior to the foramen lacerum posterius on both sides of the skull. A similar opening occurs on one side of F.M. No.

P13420. I believe these to be artifacts, but even if they are natural it seems doubtful that they bear any relation to the entocarotid.

In a previous paper (1932) I described what appears to be a mastoid process in this genus and *Homalodotherium*. I also described (p. 19) an adventitious bone exposed on the occiputs of certain other forms. Simpson (1936) has determined the presence of an adventitious bone (possibly two of them) in *Oldfieldthomasia* by means of serial sections, and has suggested (p. 8) that 'the supposed mastoid in *Rhynchippus* and *Homalodotherium* is in reality the adventitious element. Work on the internal structure of these forms has revealed that this suggestion is correct, the mastoid process of the periotic being small and closely applied to, but distinct from the adventitious bone.

### Leontiniidae Ameghino

*Ancylocoelus* Ameghino (fig. 51).

I have already given some notes on a specimen of *Ancylocoelus frequens* Ameghino<sup>1</sup> (1932, pp. 15, 17, fig. 4b), but these may be added to in the light of the broader comparisons made in this paper. The specimen, F.M. No. P14715, was collected by Mr. Sternberg in the Deseado beds at La Flecha, Santa Cruz, Argentina. The specimen consists of the squamosal and parts of the alisphenoid and tympanic, and exposes the middle ear in dorso-ventral transverse section. The dorso-ventral superposition of the epitympanic sinus, tympanic cavity, and hypotympanic sinus is well shown, the arrangement being very similar to that of the Toxodontidae. The very small horizontal septum is shown in section directly beneath the small, shallow, postero-medianly facing sulcus tympanicus, a further resemblance to the toxodontids. There is no trace of a crista tympanica. The small pneumatic foramen to the epitympanic sinus is visible above the sulcus tympanicus. The hypotympanic sinus, or what remains of it, is hollow. The venous sinus is well shown on the medial side of the epitympanic sinus. The figure shows one of the vascular foramina along the squamoso-parietal suture opening into it, and an opening, evidently for the passage of the lateral cerebral venous sinus, leading medially from it. The course of the stylomastoid foramen is well shown. Its internal orifice is above the posterior

<sup>1</sup> Described as *Colpodon* sp. and the horizon given as Colhué-Huapi in the paper cited. This error has been explained and corrected elsewhere (Patterson, 1935, pp. 165-166).



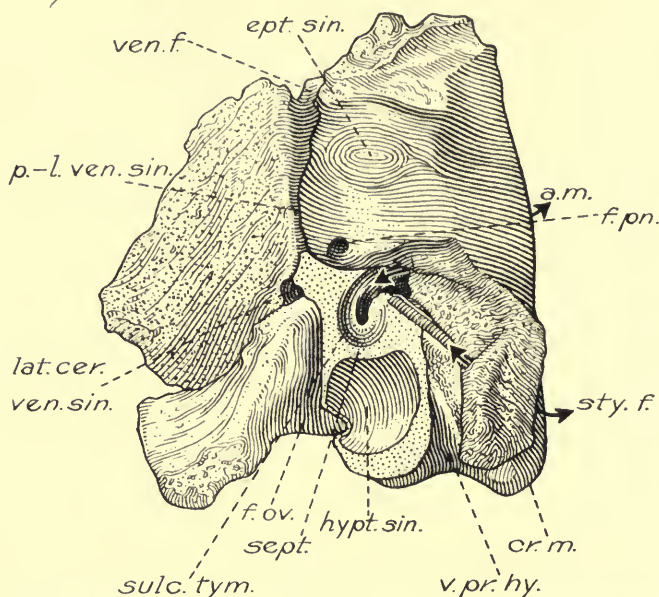


FIG. 51. *Ancylocoelus frequens* Ameghino. F.M. No. P14715. Posterior view of auditory region of right side. Dotted areas represent sectioned bone. Occipital elements lacking. For abbreviations see page 227.  $\times 2/3$ .

"leg" of the sulcus tympanicus, apparently the usual position in the order.

### *Leontinia* Ameghino.

A description of the external structure of the auditory region of this genus will be given in a paper now in preparation on the structure and affinities of the family. The internal structure, as far as revealed by the available material, is almost identical to that of the toxodontids.

### Suborder Entelonychia Ameghino

#### Homalodotheriidae Ameghino

#### *Homalodotherium* Flower (figs. 52, 53).

The magnificent specimen of *H. cunninghami* Flower,<sup>1</sup> F.M. No. P13092, collected by Mr. Riggs in the vicinity of Cape Fairweather, Santa Cruz, and previously described in several papers, was further prepared in the hope that it might reveal some details of the middle ear structure. The bullae had been broken after burial and the first preparator had merely added plaster to the broken edges. Mr.

<sup>1</sup> This specimen was identified as *segoviae* by Professor Scott. See addendum on page 225.



Quinn, however, found upon removal of this plaster that the ventral walls had been crushed up into the hypotympanic sinus and that nearly all the pieces were preserved. These he skillfully fitted together, thus giving an accurate idea of the external form. The bulla is very nearly as deep as long, and is egg-shaped in ventral

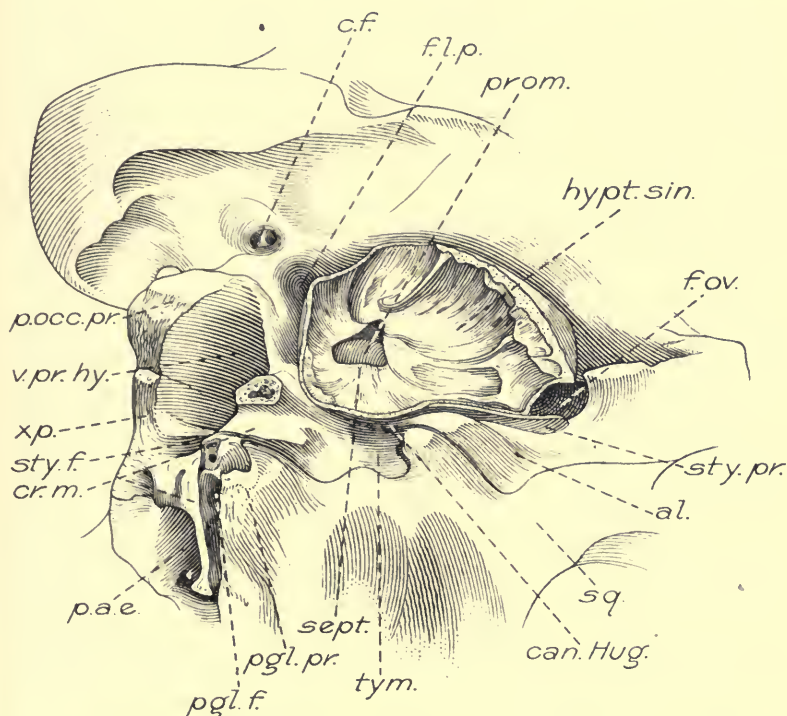


FIG. 52. *Homalodotherium cunninghami* Flower. F.M. No. P13092. Ventro-lateral view of auditory region of left side. Dotted areas represent sectioned bone. Paroccipital process weathered off. Bulla slightly displaced anteriorly. For abbreviations see page 227.  $\times 3/4$ .

view, the narrow end pointing forward. Restoration of the bullae has revealed some other features of interest in the surface morphology.

Lateral to the posterior half of the styliform process is a blunt process. The lateral portion of this is formed by the squamosal, the medial and deeper portion by the alisphenoid. The latter bone extends postero-externally in a fairly wide strip which forms the greater part of the lateral border of the fissura Glaseri. Beyond the

blunt process it contracts to a thin strip of bone which reaches nearly to the end of the fissure. The posterior extremity of the fissura Glaseri is formed by an extension from the tympanic, an exceptional feature. I have previously described (1932, p. 8) the very complicated crista meati of this specimen. That portion of the crest which partly covers the distal end of the postglenoid process extends dorsally up the medial side of this process and then flares out slightly just behind the blunt process described above (fig. 52). Medially this extension inclines sharply upward to form a groove behind the fissura Glaseri and lateral to the wall of the bulla with which the extension is continuous. The squamosal is thus entirely excluded from the fissura Glaseri. I have not encountered a comparable condition in any other notoungulate. In view of these hitherto concealed structures a new figure of the ventral view of the skull is given (fig. 53). This supersedes the figure previously published by me (1934b, fig. 23).

The hypotympanic sinus is extremely large and forms the visible part of the bulla. As in the Toxodonta, it is ventral to the tympanic cavity, in fact rather more so than in that group since it has a greater lateral extension. Its outstanding peculiarity lies in the rugose, partly cancellous walls, and the low septa which radiate from the opening communicating with the tympanic cavity. On the dorsal parts of the posterior and lateral walls there are a number of small septa, some of which begin at the opening while others arise further down the walls. None of these are very long. On the ventral parts of the posterior and lateral walls the septa become fewer and lower, and small inwardly projecting processes resembling miniature stalagmites appear. On the anterior portion of the floor of the sinus two major septa extend forward from the opening. One of these proceeds anteriorly, the other antero-internally. Between them at their extremities other smaller processes occur, the whole forming an intricate network of septa and cellulae in the antero-internal part of the sinus. The medial half of the ventral wall bears large irregular septa. The fine septa on the walls of the sinus of *Rhynchippus pumilus* constitute the only approach to this condition in any of the other genera studied. In the vicinity of the opening to the tympanic cavity, the roof of the sinus does not rest directly upon the ventral surface of the promontorium, but is separated from it by a shallow recess. As in the Toxodonta, the tympanic cavity and hypotympanic sinus are partially separated by a small horizontal septum lying beneath the sulcus tympanicus.

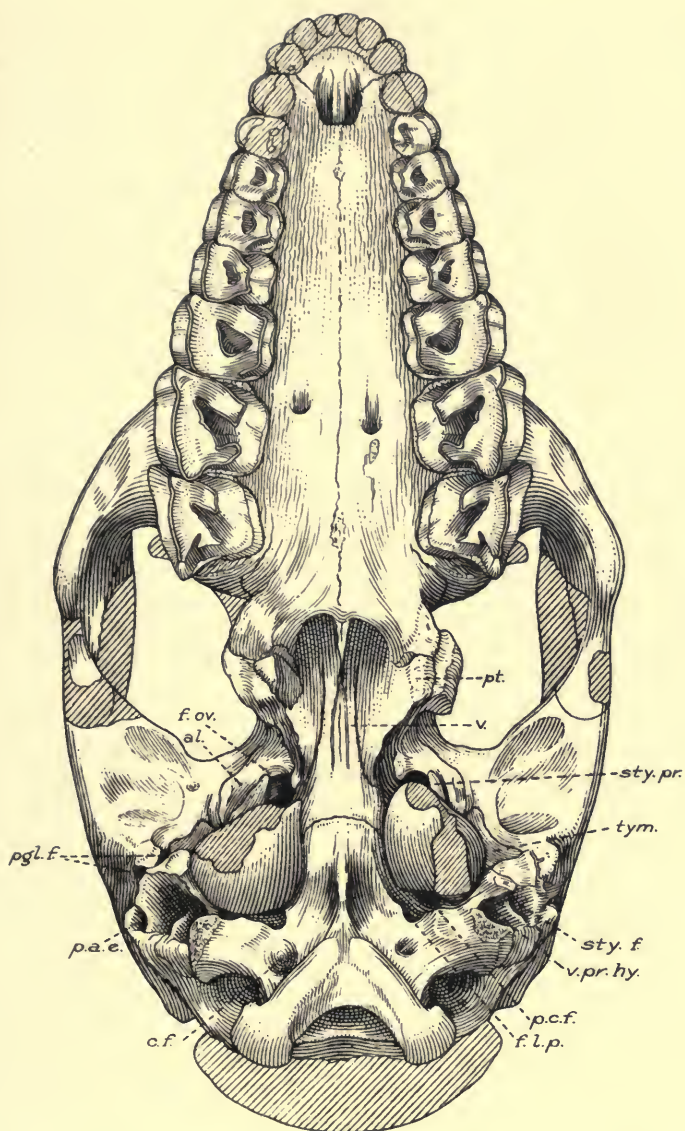


FIG. 53. *Homalodotherium cunninghami* Flower. F.M. No. P13092. Cross-hatched areas restored from Scott's figure. Left bulla slightly displaced anteriorly. *pt.*, pterygoid; *v.*, vomer; for other abbreviations see page 227.  $\times 1/3$ .



The tympanic cavity, although not fully revealed, appears to be definitely smaller than the hypotympanic sinus. A well-developed freely projecting styliform process is present which, as in the toxodonts, does not unite with the lateral wall of the hypotympanic sinus. The promontorium appears to be relatively smaller than in the other forms described.

The posterior carotid foramen and the external orifice of the stylomastoid foramen have been described previously. The external opening of the canal of Huguier is bounded posteriorly by the tympanic extension described above. No other details of the circulatory or nervous systems are revealed, but they are doubtless similar to those of the toxodonts.

### AUDITORY OSSICLES

The most disappointing feature of the present study has been the small number of ossicles encountered. Only five of these bones were found: An incus from a specimen of *Nesodon imbricatus* Owen, F.M. No. P12064, collected by Mr. H. T. Martin at Río Gallegos, Santa Cruz; and the malleus and incus from two individuals of *Adinotherium ovinum* (Owen), F.M. Nos. P13110 (described above) and P13231, collected by Mr. Abbott on the Atlantic coast twelve miles south of Río Coyle, Santa Cruz.

*Malleus* (fig. 54).—The head as a whole is very robust, and extends forward far in advance of the dorso-ventral axis of the neck. The portion of the head above the articular surface is large, smooth, convex, and irregularly oval in outline. It projects farther on the internal than on the external side. The antero-posterior diameter is rather greater than the transverse; the transverse diameter is greatest posteriorly. The articular surface for the incus is approximately one and one-half times as broad as it is deep. The two facets form a deep concavity with an angle of about 120°, and are separated at their centers by a groove. The upper has an irregular proximal border and is excavated distally. The external half of the facet is gently convex, the internal half gently concave. The lower facet is not as wide transversely as the upper but is somewhat deeper; its proximal border is arched to conform with the distal outline of the upper facet. The entire surface is gently convex.

The neck is straight, stout and short; the antero-posterior diameter is slightly greater than the transverse. The external face bears a small forwardly directed process situated midway between the head and the processus brevis. A very small lamina is present on

the anterior face which does not project out from beneath the head. The major portion of the lamina is situated beneath the anteriorly projecting portion of the head and is strongly convex ventrally. This portion is continuous with a smaller and straighter part which extends anteriorly from the neck. There is no processus gracilis. Between the head and the lamina is a deep concavity which continues distally as a groove in the internal face of the neck, ending in a

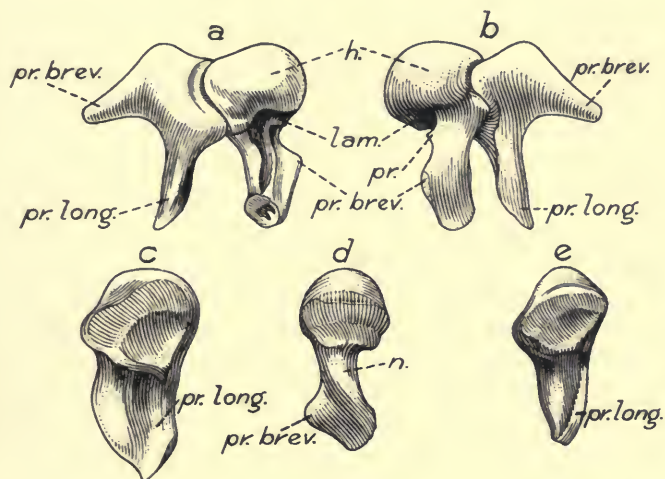


FIG. 54. Auditory ossicles of left side. For abbreviations see page 227.  $\times 4/1$ . a, *Adinotherium orinum* (Owen). F.M. No. P13231. Medial view of malleus and incus. b, The same. Lateral view of malleus and incus. c, *Nesodon imbricatus* Owen. F.M. No. P12064. Anterior view of incus. d, *Adinotherium orinum* (Owen). F.M. No. P13231. Posterior view of malleus. e, The same. Anterior view of incus.

foramen slightly below the level of the processus brevis. This process is compressed antero-posteriorly and is quite prominent. No processus muscularis is visible on the part preserved.

The manubrium is almost entirely missing. The preserved proximal extremity is considerably compressed; its maximum transverse diameter is directed postero-internally.

*Incus* (fig. 54).—This bone is so similar in *Adinotherium* and *Nesodon* that separate descriptions are not necessary. The proportionate size of incus to malleus is approximately the same as in the primates. The body is stout and approximately one and one-third times as deep as it is wide. The articular surface is an exact counterpart, in reverse, of that on the malleus. A slight difference occurs between *Nesodon* and *Adinotherium* in the contour of the

proximal border of the upper facet. A groove surrounds its internal, proximal, and lateral margins. The external surface of the body is nearly plane, the internal surface is rather more rounded. The processus brevis is short, straight, and quite slender. In *Nesodon* it is nearly circular in section; in *Adinotherium* slightly compressed laterally. The processus longus is compressed antero-posteriorly, concave anteriorly, and convex posteriorly. It is slightly bowed anteriorly and the distal portion turns inward. In *Adinotherium* the external and internal sides taper evenly towards the distal end, but in *Nesodon* the internal side is very heavy and decidedly convex, imparting to the process a considerable transverse diameter. The distal extremity of the processus longus is unfortunately broken off in all specimens. The two processes are not strongly divergent.

A careful perusal of the classic work of Doran (1878) has failed to reveal any existing form that is closely comparable to *Nesodon* and *Adinotherium*. In view of the taxonomic position of the Notoungulata, this is not surprising. Before useful comparisons can be made, knowledge of the ossicles of the Condylarthra and other primitive ungulate orders will be necessary, a seemingly remote possibility at present. It may perhaps be emphasized that the ossicles described above show no important resemblances to, and many differences from those of the Hyracoidea (*Procavia* has been directly compared). This is of some interest in connection with the now generally discredited hypothesis of direct typothero-hyracoid relationships.

### THE SEPTUM IN THE BULLA

Among the various septa which may occur in the bulla is one known as the septum bullae formed by union of ecto- and entotympanic elements. This septum "always shows a free upper margin, the rostral, under, and caudal margins being attached to the bulla," and never "runs inward from the sulcus tympanicus" (Van der Klaauw, 1931, p. 210). The septa of *Hegetotherium* and *Pachyrhinos* fulfill these requirements so completely that I had no hesitation in stating in a previous paper (1934a, p. 84) that the bulla was compound. Conditions in other genera, however, are not identical. The septum is not present in the Interatheriidae and Typotheriidae, although vertical ridges which might be remnants of it do occur. In the Toxodonta and *Homalodotherium* the septum is greatly reduced in size and horizontal in position. Provided that this small ridge is not a neomorph, it is homologous with the hegetotherid septum since in that family the hypotympanic sinus is lateral to the



tympanic cavity and the septum consequently vertical, while in those forms in which the septum is horizontal the hypotympanic sinus is below the tympanic cavity. The large size of the hypotympanic sinus in the *Toxodonta* and *Homalodotherium*, and its sharp demarcation from the tympanic cavity, could be regarded as evidence that it was formed by a separate element.

*Oldfieldthomasia*, the only Casamayor genus and the only notio-progonian in which the middle ear structure is known, shows no structure that could be definitely regarded as a septum bullae (Simpson, 1936, p. 14). Since the Notioprogonia as a group are ancestral to the surviving later families, it might be concluded that the lack of a septum bullae in *Oldfieldthomasia* indicated that the notoungulate bulla was not compound and that the septa described in this paper were not due to union of ecto- and entotympanics. On the other hand it is possible that *Oldfieldthomasia* has secondarily lost the septum. Until the middle ear structure of other notioprogonians is known, it will be impossible to arrive at a decision between these alternatives. The hegetotherid septa and the very distinct hypotympanic sinus of the *Toxodonta* nevertheless incline me to believe that the bulla is compound. The evidence at present available, however, is not complete enough to justify my somewhat too positive earlier statements.

### SUMMARY

The external characters of the auditory region are comparatively uniform throughout the order. It was therefore somewhat surprising to find, as this investigation progressed, that the internal structure showed greater diversification than had been expected. The differences and resemblances between the various families are of considerable taxonomic interest.

*Characters common to all forms described.*—Well-developed hypotympanic sinus; Eustachian tube opening postero-lateral, or posterior to the foramen ovale and situated at the anterior extremity of the tympanic cavity (surrounded by the tympanic in all forms described here in which this detail could be observed, but bounded dorsally by the periotic in *Oldfieldthomasia* (Simpson, 1936, p. 17); epitympanic sinus in the squamosal connected by the foramen pneumaticum with the recessus epitympanicus; course of the facial nerve and chorda tympani essentially as described by Simpson for *Oldfieldthomasia* and above for *Hegetotherium*, probably only minor variations of this arrangement occurring in the order; conspicuous postero-lateral venous sinus situated antero-internal to the epitympanic sinus and

receiving cerebral venous sinuses, the postglenoid foramen or foramina, the various venous foramina distributed along the squamosoparietal suture, and the mastoid foramen; small mastoid process of periotic.

Some additions and subtractions may be necessitated by future work, but it seems likely that these features will in the main be found characteristic of the order as a whole.

*Distinctive characters of the Hegetotheriidae.*—A vertical septum in the bulla between the tympanic cavity and the hypotympanic sinus, the septum being attached to the bulla anteriorly, ventrally and posteriorly; no styliform process; relatively well-developed crista tympanica; internal carotid artery did not traverse the bulla.

*Distinctive characters of the Interatheriidae and Typotheriidae.*—No septum in the bulla (vertical ridges that may be vestiges of this structure have been noted above), the separation of the tympanic cavity and the hypotympanic sinus consequently not as distinct as in other groups; a tendency in both families towards a filling in of the hypotympanic sinus by cancellous enlargement of its medial wall;<sup>1</sup> styliform process present or secondarily lost (e.g. *Interatherium robustum*), when present appressed to the anterior end of the bulla; low crista tympanica; internal carotid artery traversed the bulla.

In a previous paper (1934c, pp. 135–136) I suggested on the basis of certain external characters that the Interatheriidae and Typotheriidae were perhaps more closely related to each other than to the Hegetotheriidae. It was very gratifying therefore to find that this suggestion was strongly supported by the middle ear structure. Derivation of the *Typotheriopsis* or *Pseudotypotherium* middle ear from a type such as that of *Prototypotherium australe* would involve only a slight dorsal migration of the tympanic cavity.

*Distinctive characters of the Toxodonta and Homalodotherium.*—Hypotympanic sinus as large as or larger than the tympanic cavity and ventral to it, these cavities forming with the epitympanic sinus a dorso-ventral row of three interconnecting chambers; a small horizontal septum between the tympanic cavity and the hypotympanic sinus; a projecting, laterally compressed styliform process usually present; internal carotid artery traversed the bulla.

The present study was completed at this time in an attempt to discover deep-seated differences between the Toxodonta and En-

<sup>1</sup> The medial wall is also enlarged in *Pachyrhinos moyani*, but, as stated above, the cancelli are of a different type.



telonychia which might aid in determining the subordinal position of the leontiniids. The notohippids were found to resemble the toxodontids in middle ear characters, while the leontiniids were found to agree more closely with the toxodontids in both external and internal characters than with any other family. It appeared likely that as far as the ear was concerned the Leontiniidae would fall naturally into the suborder Toxodonta. *Homalodotherium* was then sectioned in the confident expectation of finding characters at least as striking as those separating the "toxodont" middle ear type from either of the typotherian types. Greatly to my surprise, however, this genus, so unique in skeletal characters and so different from the toxodontids in the external appearance of the auditory region, did not differ from the Toxodontidae in any internal character of importance. *Homalodotherium* is if anything somewhat further advanced along the "toxodont" line of specialization than any other form studied, in that it has a larger, more laterally extended hypotympanic sinus. The rugose interior of the sinus is not developed in any of the toxodontids or leontiniids studied, but is present to a lesser degree in the notohippid *Rhynchippus pumilus*. It may be stated, therefore, that on the basis of middle ear structure, a highly important criterion, the homalodotherids stand in about the same relation to the Toxodonta as the chalicotherids do to the less aberrant perissodactyls. The effect that this finding may have on the current classification of the Notoungulata or on the subordinal status of the Leontiniidae can not be decided at present.

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#### ADDENDUM

Professor Scott in his memoir on the Field Museum skeleton of *Homalodotherium* (Field Mus. Nat. Hist., Geol. Mem., I, p. 7, 1930) referred the specimen to *H. segoviae* (Ameghino), a reference which has been repeated by me in preceding papers of this volume. It was decided recently to mount the specimen, and during the reconstruction of the eroded cranial roof some questions of proportion led to an examination of the specific determination. As a result, it was found that the skeleton should be referred to *H. cunninghami*, the genotypic species, rather than to *segoviae*. The most striking distinction between the two species lies in the greatly reduced P<sup>1</sup> of *segoviae* (Scott, 1912, p. 284, pl. 28). In P13092 this tooth is well developed, as in *cunninghami* (fig. 51; Scott, 1912, pl. 29, fig. 3). The difference in the condyles mentioned previously by me (1934b, p. 117) may well prove to be a further specific distinction.

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## ABBREVIATIONS ON FIGURES

a.c.f.	anterior carotid foramen
al.	alisphenoid
a.m.	auditory meatus
apt.tym.can.fac.	apertura tympanici canalis facialis
(?)br.sty.art.	(?)groove for branch of stylomastoid artery
c.f.	condylar foramen
can.Hug.	canal of Huguier
car.f.	carotid foramen
cr.m.	crista meati
cr.tym.	crista tympanica
crl.cav.	cranial cavity
E.f.	Eustachian tube
ept.sin.	epitympanic sinus
f.l.p.	foramen lacerum posterius
f.ov.	foramen ovale
f.pn.	foramen pneumaticum
fen.coch.	fenestra cochlearis
fen.vest.	fenestra vestibuli
h.	head
hypt.sin.	hypotympanic sinus
lam.	lamina
lat.cer.ven.sin.	lateral cerebral venous sinus
mas.	mastoid process
n.	neck
p.a.e.	porus acusticus externus
p.c.f.	posterior carotid foramen
par.-occ.sut.	parieto-supraoccipital suture
per.	periotic
pgl.f.	postglenoid foramen
pgl.pr.	postglenoid process
p.-l.ven.sin.	postero-lateral venous sinus
p.occ.pr.	paroccipital process (sectioned)
pr.	process on neck of malleus
pr.brev.	processus brevis
pr.long.	processus longus
prom.	promontorium
rec.ept.	recessus epitympanicus
sept.	septum in the bulla
sq.	squamosal
sty.f.	stylomastoid foramen
sty.pr.	styliform process
sulc.fac.	sulcus facialis
sulc.tym.	sulcus tympanicus
tym.	tympanic
tym.cav.	tympanic cavity
v.pr.hy.	vagina processus hyoidei
v.r.	vertical ridges in the bulla, possibly vestiges of the septum
vasc.f.	unidentified foramina, probably vascular
ven.f.	venous foramina opening externally on or near the squamoso-parietal suture
xp.	posterior adventitious bone





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